动 物 学 研 究 2007, Feb. 28(1): 41-46 CN 53-1040/Q ISSN 0254-5853
Zoological Research

Competitive Strategies of Two Species of Co-occuring Tadpoles

ZHANG Jin-dong[1,2], XIONG Ye[1], FU Zhi-ping[2],
LI Yu-jie[3], DAI Qiang[1], WANG Yue-zhao[1,*]

(1. *Chengdu Institute of Biology, the Chinese Academy of Sciences, Chengdu* 610041, *China*;
2. *The North-west Sichuan Eucational Research Center of Giant Panda Protection, Mianyang Normal University, Mianyang* 621000, *China*;
3. *College of Life Science, China West Normal University, Nanchong* 637002, *China*)

Abstract: We examined the competitive ability of larval toads (*Bufo gargarizans*) and frogs (*Rana kukunoris*) which co-occur in natural pools in the Jiuzhaigou Nature Reserve. We measured the activity level, growth rate, mass at metamorphosis and larval period in a laboratory experiment. Tadpoles of *B. gargarizans* were significantly more active when food was abundant than scarce, while there was no significant difference in the activity of *R. kukunoris* tadpoles at different food levels. At low food availability, mass at metamorphosis and growth rate of *R. kukunoris* were significantly increased in the presence of *B. gargarizans*, whereas the presence of *R. kukunoris* had no significant effect on the mass and growth rate of *B. gargarizans*. In all treatments, the larval period of *B. gargarizans* at low food availability was the shortest. These results suggest that *B. gargarizans* can adapt to different food levels by changing their activity rate. At high food level, *B. gargarizans* increased activity to gain more food. At low food level, *B. gargarizans* decreased activity and achieved early metamorphosis. However, when food resources were limited, *R. kukunoris* could gain more food than *B. gargarizans*.

Key words: Activity level; Mass at metamorphosis; *Bufo gargarizans*; *Rana kukunoris*; Interspecific competition

同水塘分布两种无尾两栖类蝌蚪的竞争策略

张晋东[1,2], 熊 晔[1], 傅之屏[2], 李玉杰[3], 戴 强[1], 王跃招[1,*]

(1. 中国科学院成都生物研究所, 四川 成都 610041;
2. 绵阳师范学院 川西北大熊猫教育研究中心, 四川 绵阳 621000;
3. 西华师范大学 生命科学学院, 四川 南充 637002)

摘要: 实验室条件下, 通过活动性水平, 变态时的体重、增长率和完成变态所需时间考察同水塘分布的中华蟾蜍(*Bufo gargarizans*)和高原林蛙蝌蚪(*Rana kukunoris*)的竞争策略。实验按照 2×3 因子设计, 即: 食物资源 2 个水平(高、低), 组合方式 3 个水平(10 只中华蟾蜍蝌蚪, 记为 B 组; 5 只中华蟾蜍蝌蚪和 5 只高原林蛙蝌蚪, 记为 BR 组; 10 只高原林蛙蝌蚪, 记为 R 组)。中华蟾蜍蝌蚪的活动性在食物水平低时显著低于食物水平高时, 而高原林蛙蝌蚪的活动性在不同食物水平下无显著差异; 食物水平低时, 混合组的高原林蛙蝌蚪变态时体重和体重增长率都显著高于 R 组, 而混合组中华蟾蜍蝌蚪与 B 组相比无显著差异; 在不同处理组中, 食物水平低时混合组中华蟾蜍蝌蚪幼体期最短。这些结果表明: 中华蟾蜍蝌蚪在不同食物资源条件下所选择的生存策略可能不同, 即食物资源充足时, 增加活动性获取更多食物; 食物资源有限时, 降低活动性且提前完成变态; 与中华蟾蜍蝌蚪相比, 在食物资源有限时高原林蛙蝌蚪获取食物能力更强。

关键词: 活动性水平; 变态时体重; 中华蟾蜍; 高原林蛙; 种间竞争
中图分类号: Q959.5 **文献标识码:** A **文章编号:** 0254-5853(2007)01-0041-06

Received date: 2006-10-03; Accepted date: 2006-12-22
* Corresponding author(通讯作者), E-mail: arcib@cib.ac.cn
收稿日期: 2006-10-03; 接受日期: 2006-12-22
基金项目: 国家自然科学基金资助项目(30470252)
第一作者简介: 张晋东(1978-), 男, 硕士, 助教, 主要从事保护生物学研究。E-mail: zhangjd224@163.com

Anuran larvae are useful models for the study of community ecology because they are easy to sample and have readily quantifiable fitness attributes, including growth rate and survival to metamorphosis (Werner, 1992, 1994; Pearmann, 1995; Bardsley & Beebee, 1998).

Experimental manipulations of life-history traits of different larval anurans, including growth, mass at metamorphosis and date of metamorphosis, were used as measures of response to inter- or intra-specific competition. The overall distribution and competitive ability of tadpoles in the field was not considered. Recently, field investigations have combined the distribution of tadpoles with laboratory experiments (Laurila, 2000). Generally, larvae of species that are characteristic of temporary pools are more active, and have higher growth and development rates, than those in permanent pools. Species typical of temporary pools have been considered superior competitors and can have negative effects on permanent pool species (Denver, 1997). Some ecologists have investigated whether the distribution of tadpole can be related to the results of the laboratory experiments, and postulated that factors like pond hydroperiod and predation (Bardsley & Beebee, 1998) and use of microhabitat (Richter-Boix, 2004) were important in determining the structure of anuran communities in the field. Laurila (2000) designed laboratory and field experiments to test the hypothesis that temporary pool species negatively affect permanent pool species. Laurila (2000) hypothesised that the factors affecting the distribution of anuran larvae would be more dependent on the interplay between available resources and reproductive effort, or on the physical factors of pools, than on competitive interspecific interactions.

In Laurila's experiment, anuran egg clumps were collected from different pools, and different developmental stages of tadpoles were used, however the experiment ignored temporal competition. This paper examines the competitive strategies of larval toads (*Bufo gargarizans*) and frogs (*Rana kukunoris*) which co-occur in natural pools. Using laboratory experiments, we manipulated the density of tadpoles of these two species, of approximately the same development stages, to investigate competition for food. During field experiments, we measured the surface area and depth of pools, and the number of the two tadpole species occurring in the pools, to analyse the relationship of the distribution patterns and competitive abilities of tadpoles in the laboratory.

1 Materials and Methods

The two anuran species (*Bufo gargarizans* and *Rana kukunoris*) are mainly distributed between 2 000 m and 3 000 m in the Jiuzhaigou Nature Reserve of Sichuan Province, and are both 'explosive' breeds (Li et al, 2004). We measured the surface area and depth of 14 pools containing both species of tadpole, upriver of Heye village during April 2005. At the same time, tadpoles of both species were collected from nine of these pools. The tadpoles were brought into the laboratory and raised in nine plastic containers (26 cm × 19 cm × 11 cm) filled with tap water and allowed to stand for two days. The temperature of the water was kept between 22.5℃ and 24.5℃. Tadpoles were fed goldfish food. We tested the amount of food the tadpoles could eat a week before the experiment. Three treatments were used to identify the amount the tadpoles could eat (low, 0.025 g/tadpole; medium, 0.05 g/tadpole; high, 0.075 g/tadpole), with each treatment repeated three times. The results suggested that tadpoles each consume approximately 0.025 g of goldfish food each day. *Bufo gargarizans* and *R. kukunoris* tadpoles consume approximately the same amount.

We measured the body weight of tadpoles before the experiment; at that time *B. gargarizans* tadpoles weighed 0.062 ± 0.003 g ($\pm$ *SE*) and *R. kukunoris* tadpoles weighed 0.062 ± 0.003 g ($n = 60$ in each case). All tadpoles were at developmental stages 26–28 (possessing small limb buds; Gosner, 1960).

1.1 Experimental design

The experimental arrangement was a 2 × 3 factorial design. The two factors were food level (low or high) and the presence of tadpoles of the other species. For each tadpole type there were two different competition treatments: (1) single species (2) mixed species (Tab. 1). The numbers of tadpoles used in competition treatments are presented in Tab. 1. This resulted in 36 containers of tadpoles. There were six experimental units for each treatment type.

Experimental tadpoles were placed in plastic containers (26 cm × 19 cm × 11 cm) which were filled with tap water on 28th April, and allowed to stand for two days. During experiments, approximately 80% of the water in each container was changed weekly. All treatments were carried out indoor under natural illumination and photoperiod. The temperature in the laboratory was maintained between 22.5℃ and 24.5℃.

Tadpoles were fed goldfish food at a low (0.25 g/container/day) or a high rate (0.5 g/container/day).

Tab. 1　Numbers of tadpoles in competition treatments in the laboratory experiment

	Treatments					
	B1	BR1	R1	B2	BR2	R2
Bufo gargarizans	10	5	0	10	5	0
Rana kukunoris	0	5	10	0	5	10
Total	10	10	10	10	10	10

BR: B + R; 1: Food level low; 2: Food level high.

During the first two weeks, food was delivered to the tadpoles at 3 – 4 days intervals. The amount of food was adjusted at each feeding time to tadpole numbers and tadpole weight.

1.2　Behavioural and physical variables

After two days, we started observing and recording the behaviour of the tadpoles. The observations were always made between 11:00 and 14:00. We measured behaviour through visual scanning, spending approximately 10 seconds observing each containerand completing observation of the 36 containers in six minutes. Observations of each container were repeated ten times. Two types of behaviour were recorded: activity and immobility.

Activity was recorded when over 50% of tadpoles in the container were active; immobility was recorded when over 50% of tadpoles in the container were not active.

The physical variables measured were as follows: body length (mm), mass at metamorphosis (g) and time to metamorphosis (days). Containers were checked several times daily for metamorphosing individuals. At metamorphosis [emergence of the first forelimb, stage 42 (Gosner, 1960)], individuals were removed from the containers and weighed to the nearest 1 mg and the date was recorded. The experiment ended on 13th of June with the last tadpole achieving metamorphosis.

1.3　Statistical analysis

All statistical tests were conducted on container means to avoid pseudoreplication. We compared the activities of the two species of tadpoles at different food levels. As behavioural data was expressed as a proportion, data was square-root transformed and then was arcsin-transformed before analysis. A Kolmogorov-Smirnov test was used to assess the normality of the data. When the data complied with normality, differences between individual treatments were compared using parametric tests (t-test). Conversely, when data did not comply with normality, non-parametric tests (Mann-Whitney U) were used to compare the activities of different treatments.

Similarly, Kolmogorov-Smirnov tests were used to to assess the normality of mass at metamorphosis and time of metamorphosis. Non-parametric or parametric tests were then used accordingly.

2　Results

2.1　Activity

Tadpoles of *Bufo gargarizans* were more active than tadpoles of *Rana kukunoris* at both levels of food intake (high food level: $U = 1286.5$, $P < 0.001$; low food level: $U = 1286.5$, $P < 0.001$). *Bufo gargarizans* tadpoles were significantly more active when food was abundant ($U = 1222.0$, $P < 0.001$), while the activity of *R. kukunoris* tadpoles did not differ significantly at different food levels (Fig. 1).

2.2　Growth rate

Rana kukunoris tadpoles had higher growth rates at high food level than at low food level ($t = -3.139$, $df = 97$, $P = 0.002$). At low food availability, growth rate of *R. kukunoris* were significantly increased in the presence of *B. gargarizans* ($t = -2.627$, $df = 69$, $P = 0.011$), whereas the presence of *R. kukunoris* had no significant effect on the mass and growth rate of *B. gargarizans* (Fig. 2).

2.3　Mass at metamorphosis

At low food availability, the mass at metamorphosis of *R. kukunoris* was significantly increased in the presence of *B. gargarizans* ($t = -2.268$, $df = 69$, $P = 0.026$). The mass at metamorphosis of *B. gargarizans* was decreased in the presence of *R. kukunoris*. However at high food availability the situation was reversed; the mass at metamorphosis of *R. kukunoris* was decreased in the presence of *B. gargarizans* and the mass at metamorphosis of *B. gargarizans* was increased in the presence of *R. kukunoris* (Tab. 2, Fig. 3).

2.4　Time to metamorphosis

The time to metamorphosis of the two species of tadpole was significantly different ($t = -10.319$, $df = 287$, $P < 0.001$). The average time to metamorphosis

of *B. gargarizans* was 23.89 ± 0.34 days, whereas the average time to metamorphosis of *R. kukunoris* was 30.13 ± 0.49 days. In general, the larval period of the two species of tadpole was shorter at low food level. The larval period of the two species of tadpole was also shorter in mixed groups (Fig. 4).

2.5 Interaction between competition treatments and food level

The mass of tadpoles at metamorphosis was significantly increased at a high food level ($F = 7.041$, $P = 0.008$) (Fig. 3, Tab. 3). A marginally significant ($F = 2.957$, $P = 0.054$) interaction between competition treatments and food level suggests that different treatment groups and food levels can affect mass at metamorphosis (Adjusted $R^2 = 0.58$, Tab. 3).

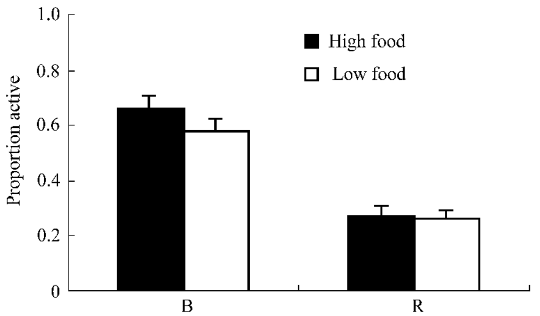

Fig. 1 Activity of *B. gargarizans* (B) and *R. kukunoris* (R) at different food resource levels

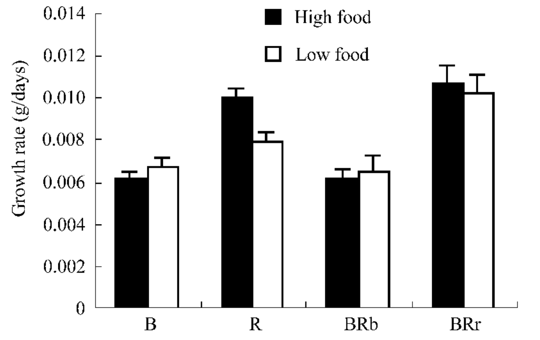

Fig. 2 Growth rate of the two species of tadpole in different treatments

B: *B. gargarizans* of group B; R: *R. kukunoris* of group R; BRb: *B. gargarizans* of mixed groups; BRr: *R. kukunoris* of mixed groups.

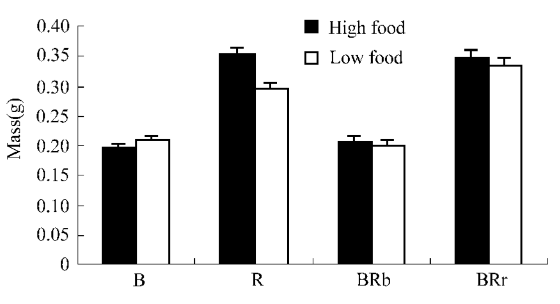

Fig. 3 Mean mass of the two species of tadpole in different treatments

B: *B. gargarizans* of group B; R: *R. kukunoris* of group R; BRb: *B. gargarizans* of mixed groups; BRr: *R. kukunoris* of mixed groups.

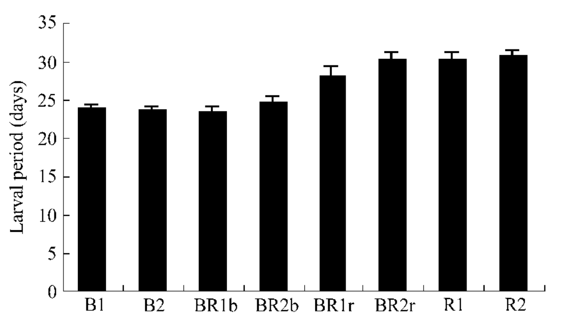

Fig. 4 Time to metamorphosis of the two species of tadpole from the start of the experiment to the 42nd development stage

B: Single *B. gargarizans* group; R: Single *R. kukunoris* group; BRb: *B. gargarizans* of mixed groups; BRr: *R. kukunoris* of mixed groups; 1: Food level low; 2: Food level high.

Tab. 2 Independent-sample t tests of the mean mass of the two species of tadpole in different treatments

Source	Mass(g)	*t*	*df*	*P*
B1 vs BR1b	0.2096 vs 0.2007	0.734	64	0.456
B2 vs BR2b	0.1974 vs 0.207	−0.955	72	0.343
R1 vs BR1r	0.2957 vs 0.3328	−2.268	69	0.026*
R2 vs BR2r	0.3539 vs 0.3462	0.466	71	0.643

* $P < 0.05$.

Tab. 3　MANOVA table of mass of 42nd stage tadpoles, treatment groups and diet level of the two species of tadpole

Source	*df*	Mean quare	*F*	*P*
Treatment groups	2	0.003	1.078	0.342
Food level	1	0.022	7.041	0.008**
Species	1	0.423	136.853	0.000***
Treatment groups × Food level	2	0.009	2.957	0.054
Species × Food level	1	0.000	0.092	0.762

Adjusted $R^2 = 0.58$; $^{**}P < 0.01$, $^{***}P < 0.001$.

3　Discussion

3.1　Competitive strategies of the two species tadpole in the laboratory

Competition takes place when limited resource availability does not allow maximal growth rate of all individuals in a population. Studies of the factors affecting the competitive ability of tadpoles have focused mainly on two flexible characters, body size and activity (Laurila, 2000). High activity may increase the competitive ability of a species by improving their harvesting rate and therefore depleting of the resources (Werner, 1992). However, foraging activity may also be affected by the amount of food available (Anholt & Werner, 1995). This paper discusses the competitive strategies of two species of tadpoles, based on mass at metamorphosis, growth rate, activity and time to metamorphosis.

The results of the laboratory experiment suggested that interspecific competition affected both *Bufo gargarizans* and *Rana kukunoris* (Tab. 3). At high food level, tadpoles of *B. gargarizans* were significantly more active than at low food level and the mass and growth rate of *B. gargarizans* increased in the presence of *R. kukunoris*. However at low food level the situation was reversed. Furthermore, at low food level, the larval period of *B. gargarizans* in mixed groups was the shortest of all treatments. These results suggest that tadpoles of *B. gargarizans* may select strategies corresponding to food availability. At high food level, tadpoles of *B. gargarizans* increased their activity to gain more food. When food was scarce, tadpoles of *B. gargarizans* decreased their activity, spent less energy on gaining food and could therefore pass through metamorphosis more quickly. In other words, changing food availability may lead to a trade-off between the advantages of gaining more food and the advantages of shorter metamorphic duration.

There was no significant difference between the activity of tadpoles of *R. kukunoris* at different food levels. At low food level, the mass and growth rate of *R. kukunoris* increased in the presence of *B. gargarizans*. There were two possible ecological explanations. Firstly, the competitive interactions between *B. gargarizans* and *R. kukunoris* appeared asymmetric. The growth rate and mass at metamorphosis of *R. kukunoris* were higher in the presence of *B. gargarizans*, indicating that *R. kukunoris* were able to maintain competitive superiority at relatively low food availability. An alternative explanation might be that in nature, the amount of food needed by the two species of tadpole is not equal. *Rana kukunoris* was able to get enough food at low food level. This explains why the activity of *R. kukunoris* tadpoles did not change at different food levels.

3.2　Relationship between field distribution and competitive ability

The competitive ability of the tadpoles in the laboratory might affect the field distribution of the two species. In field investigations, we found that the two species of tadpole co-occur in almost ever pool, whether the pool was deep or shallow, or had large or small surface area (unpublished data). We even found thousands of dead eggs and tadpoles of both species in dry pools. Laboratory results indicated also that there are other factors affecting the field distribution in addition to the competitive ability in the laboratory (MANVOA, adjusted $R^2 = 0.58$). It has been postulated that other factors, such as predation and pond hydroperiod (Bardsley & Beebee, 1998) and use of microhabitat (Richter-Boix, 2004), are more important in determining the structure of anuran communities in the field. In Jiuzhaigou Nature Reserve, the landform is relatively complex, and the altitude of anuran distribution is relatively high. Furthermore, Jiuzhaigou Nature Reserve is a famous tourist site, and human activity may affect an anuran's choice of reproductive sites. The activity and range of *B. gargarizans* and *R. kukunoris* are limited in the Jiuzhaigou Nature Reserve. This may be one reason that the two species often co-occur in pools.

Acknowledgements: Teacher LI Cheng and Teacher LIU Zhi-jun of Chengdu Institute of Biology, the Chinese Academy of Sciences helped in the field investigation, Mr. XIAO Wei-yang of Jiuzhaigou Nature Reserve Administration took part in field investigation,

Mr. CHEN Qin of Chengdu Institute of Biology, the Chinese Academy of Sciences helped in laboratory experiment. We thank them for their help and assistance.

References:

Alex RB, Gustavo AL, Albert M. 2004. Responses to competition effects of two anuran tadpoles according to life-history traits[J]. *Oikos*, **106**: 39 – 50.

Anholt BR, Werner EE. 1995. Interaction between food availability and predation mortality mediated by adaptive behavior[J]. *Ecology*, **76**: 2230 – 2234.

Bardsley L, Beebee TJC. 1998. Interspecific competition between *Bufo* larvae under condition of community transition[J]. *Ecology*, **79**: 1751 – 1759.

Gosner KL. 1960. A simplified table for staging anuran embryos and larvae with notes on identification[J]. *Herpetologica*, **16**: 183 – 191.

Laurila A. 2000. Competitive ability and the coexistence of anuran larvae in freshwater rock-pools[J]. *Freshwater Biology*, **43**: 161 – 174.

Li C, Sun ZY, Cai SC, Liu SY, Ran JH, Liu ZJ, Wang YZ. 2004. The herpetofaunal diversity in jiuzhaigou national nature reserve, China[J]. *Chin J Zool*, **39**(2): 74 – 77.[李 成, 孙治宇, 蔡永寿, 刘少英, 冉江洪, 刘志君, 王跃招. 2004. 九寨沟自然保护区的两栖爬行动物调查. 动物学杂志, **39**(2): 74 – 77.]

Pearmann PB. 1995. Effects of pond size and consequent predatory density on two species of tadpoles[J]. *Oecologia*, **102**: 1 – 8.

Werner EE. 1992. Competitive interactions between wood frog and northern leopard frog larvae: The influence of size and activity[J]. *Copeia*, **1**: 26 – 35.

Werner EE. 1994. Ontogenetic scaling of competitive relations: Size-dependent and responses in two anuran larvae[J]. *Ecology*, **75**: 197 – 213.

寻找差距 共谋发展
——2007 年《动物学研究》编委会会议纪要

在金猪拱年之际，在《动物学研究》踏上她的第二十八个春秋之初，在昆明动物研究所召开了 2007 年《动物学研究》编委会工作会议。我所所长、本刊主编张亚平院士，本刊英文编辑 Miss Claire Maries，在昆所外编委云南大学肖蘅教授、西南林学院的韩联宪教授、美国大自然保护协会中国项目部龙勇诚项目经理，我所 17 位编委及编辑部成员等出席了会议。

会议由我所党委书记、本刊副主编杨君兴研究员主持。首先，由编辑部主任单访同志汇报了 2006 年编辑部和编委会的工作。她主要就编辑部在稿件英文化、网络化方面所做出的成绩和存在问题，以及中国科技信息研究所提供的本刊相关指标等向编委会做了汇报；也通报所外编委对办刊设想调查的反馈意见以及编委履行职责的情况。接着，就报道范围、学科编委负责制等展开了充分地讨论。会议一致同意实行学科编委负责制。会议认为：编辑部应在组稿方面加大力度，主动出击；同时需要在所外物色和发展新的务实的学科编委，以加强编辑力量。会上，还就如何寻求刊物平衡发展、组织和选择哪方面的稿件、采取哪些措施对质量较高的论文和对本刊有贡献的审稿人给予奖励，怎样提高发表论文的显示度等，编委们提出了不少具体的指导性建议。

讨论结束后，副主编杨君兴研究员说，在新一任主编的领导下，《动物学研究》的工作有所推进，但是，要把她真正办好，还需要给予相当的重视；今天的会议虽短，但大家很热心，出了不少金点子，相信会把刊物再往前推进一步。最后，主编张亚平院士说，我代表研究所感谢各位编委和编辑部的工作，希望会后仍然给予更多的支持，提出更多更好的建议，继续推进《动物学研究》的发展；预祝各位新年工作顺利！身体健康！